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A NEW HYBRID MANAKIN (*DIXIPHIA PIPRA* × *PIPRA FILICAUDA*) (AVES: PIPRIDAE) FROM THE ANDEAN FOOTHILLS OF EASTERN ECUADOR

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Abstract.—A new intergeneric hybrid manakin (*Dixiphia pipra* × *pipra filicauda*) is described from the Andean foothills of eastern Ecuador. The adult male specimen represents the first record of hybridization among species belonging to different clades of the traditional but polyphyletic genus *Pipra* (Prum 1990, 1992). The collecting locality, Sarayacu (1°44′S, 77°29′W), apparently lies in a narrow zone of elevational overlap between the two parental species. The hybrid is nearly intermediate between the parental species in size, plumage pattern, and color.

The few documented cases of hybridization in neotropical manakins (Pipridae) have been between species within the same superspecies, or between species in different genera (Parkes 1961, Haffer 1967, Parsons et al. 1993). Prum's (1990, 1992) recent revision of the family indicated that the genus *Pipra,* as currently recognized (e.g., Sibley & Monroe 1990), is polyphyletic, composed of three monophyletic clades (*Pipra, Dixiphia, Lepidothrix*). Hybridization among species belonging to different "Pipra" lineages is unknown and the subject of this paper.

An enigmatic manakin was collected by M. Olalla on 21 August 1951, at Sarayacu (1°44′S, 77°29′W; Paynter & Traylor 1977), Provincia de Pastaza, Ecuador. Not clearly assignable to any described species, the specimen (Museo Ecuatoriano de Ciencias Naturales no. 2748) had been variously identified on the tag by taxonomists as a hybrid (i.e., *Pipra filicauda* × *Chiroxiphia* sp., *P. filicauda* × *Heterocercus* sp., *P. filicauda* × *P. erythrocephala*). Analyses of plumage characters and external morphology revealed that none of these hypotheses was correct: the specimen represents a hybrid between *Dixiphia pipra* (white-crowned manakin) and *P. filicauda* (wire-tailed manakin).

Materials and Methods

Sexed as a male, the specimen appears fully mature as judged by its glossy black mantle, wings, and tail. I compared it with series of all species of manakins in the Museo Ecuatoriano de Ciencias Naturales and the National Museum of Natural History, Smithsonian Institution. For the purpose of the hybrid diagnosis (see Graves 1990), I considered all species of manakins ($n = 16$) that occur in western Amazonia and the adjacent Andean foothills of Colombia, Ecuador, and Peru north of the Río Marañón as potential parental species. Measurements of wing chord, length of central rectrices (= tail), and bill length from anterior edge of nostril were taken with digital calipers. Color comparisons were made under examolites (Macbeth Corp.).

Results

Plumage characters.—Determination of parentage was facilitated by the boldly patterned plumage of the hybrid (Fig. 1) and by the small number of potential parental

Fig. 1. Ventral, lateral, and dorsal views of adult males of *Pipra filicauda* (bottom), a presumed *Dixiphia pipra* × *P. filicauda* hybrid, and *Dixiphia pipra* (top).

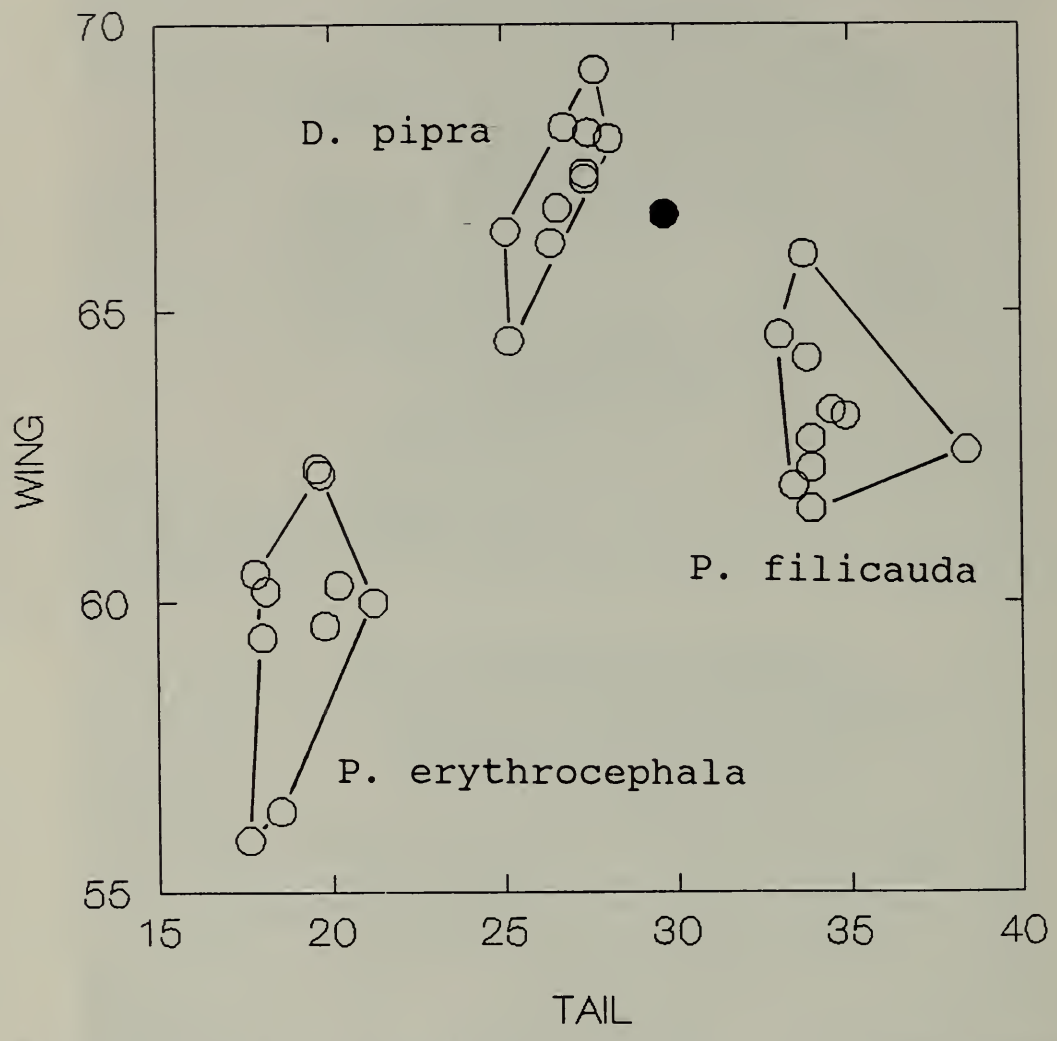

Fig. 2. Bivariate plot of wing and tail lengths (mm) of *Dixiphia pipra, Pipra filicauda, P. erythrocephala,* and a presumed *D. pipra* × *P. filicauda* hybrid (filled circle).

species. Of the many possible combinations of parental species, only one (*Pipra filicauda* × *Dixiphia pipra*) could combine to produce the diagnostic characters of the hybrid: (1) golden yellow crown and hindneck; (2) dark facial patch; (3) mottled yellow and black underparts; (4) glossy black tail, wings, and mantle; and (5) shallowly forked tail (see Appendix).

The distribution of carotenoid pigments in the plumage of the hybrid is similar to manakins in the *Pipra aureola* superspecies, including *P. filicauda.* This fact and the forked tail of the hybrid suggest that *P. filicauda* is one of its parental species. Because *P. filicauda* has an unmarked yellow face, the dark facial patch of the hybrid must have been inherited from the other parental species. The dark facial patch of the hybrid is formed by feathers of the loral and subocular areas and the auriculars. Several species of manakins in western Amazonia have black auriculars. *Xenopipo atronitens* and *Heterocercus* spp. can be eliminated from consideration because they possess structural modifications of the remiges and rectrices, respectively, that are absent in the hybrid. Likewise, the plumage of the hybrid lacks the distinctive plumage characters, even in traces, of several other potential parental species: *Lepidothrix isidorei* (blue rump patch); *Chiroxiphia pareola* (blue mantle), and *Masius chrysopterus* (frontal tuft, yellow webs of remiges and rectrices). Two remaining species with black auriculars have black body plumage and contrasting crowns: *D. pipra* (white crown) and *L. coronata* (blue crown). Although the inher-

Table 1.—Ranges and means (±one standard deviation) of measurements (mm) of adult males of *Dixiphia pipra, Pipra filicauda,* and *P. erythrocephala* from eastern Ecuador, and the hybrid, *D. pipra* × *P. filicauda.*

	(*n*)	Characters		
		Wing	Tail	Bill length
D. pipra	10	64.5–69.2 67.2 ± 1.32	25.1–28.1 26.8 ± 1.02	6.4–7.2 6.7 ± 0.25
P. filicauda	10	61.6–66.0 63.3 ± 1.33	33.0–34.3 34.3 ± 1.52	7.0–8.0 7.4 ± 0.26
P. erythrocephala	10	55.9–62.3 59.7 ± 2.10	17.6–21.2 19.1 ± 1.21	5.9–6.8 6.2 ± 0.29
Hybrid	1	67.7	29.7	7.1

itance of structural colors is poorly understood, it is probable that a hybrid of *L. coronata* would exhibit at least traces of blue on the crown. I interpreted this absence as evidence that *L. coronata* was not a parent of the hybrid. Other combinations of species either lack the range of plumage pattern elements expressed in the hybrid or possess distinctive characters not found in the hybrid. For example, the specimen in question could not represent a hybrid of *P. filicauda* and *P. erythrocephala* because neither species has black auriculars. Thus, a hybrid between *D. pipra* and *P. filicauda* is the only remaining possibility.

External morphology.—The parental hypothesis derived from plumage pattern and color was supported by a bivariate scatterplot of wing and tail length (Fig. 2). Because the specimen had once been identified as a hybrid of *P. filicauda* and *P. erythrocephala,* the latter species has been included in Table 1 for comparison. Under the assumptions used here (Graves 1990), if the specimen represents a hybrid of *D. pipra* and *P. filicauda,* then the mensural dimensions of the specimen should fall within the range of measurements of the parental species. This expectation was confirmed. Wing length of the hybrid was greater than that of either *P. filicauda* or *P. erythrocephala,* indicating that the hybrid is not a product of this combination of species. Otherwise, the hybrid would be required to exhibit both atavism (hybrid expresses characters not found in either parental species) and morphological luxuriance (hybrid is larger than either parental species). Neither phenomenon has been convincingly demonstrated in hybrids of passerine birds.

Geography.—The collection locality, Sarayacu, lies at the base of the Andes on the Río Bobonaza, a primary tributary of the Río Pastaza. The elevation of this site was not recorded on the specimen label; the airstrip at Sarayacu lies between the 300 and 600 m contour lines, approximately 40 km upslope from the 300 m contour interval and within 10 km of the 600 m contour interval (1:1,000,000 Mapa Físico, Instituto Geográphico Militar, Quito, 1991). *Pipra filicauda* is widespread in the lowlands of eastern Ecuador (recorded to 500 m elevation in Colombia, Hilty & Brown 1986). However, *D. pipra* has not been reported in Ecuador below 400 m elevation (M. B. Robbins, pers. comm.). Thus, the hybrid was apparently collected in a narrow zone of overlap between the two species.

Discussion

The hybrid exhibits a blend of parental plumage patterns rather than a mosaic of plumage elements. The one exception is the peculiar dark facial patch of the hybrid. The auricular area of both parental species is concolor with the throat and breast. Under

magnification, the auriculars and subocular feathers of the hybrid appear grizzled yellow and black. At arm's length, however, this region contrasts with the adjacent yellow plumage of the throat and crown. Inheritance of a dark facial patch has also been noted previously in another manakin hybrid, *Pipra aureola* × *Heterocercus linteatus* (Parkes 1961). These observations suggest that pigmentation of the facial region in *Pipra* manakins is controlled independently of the crown and throat.

A surprising variety of carotenoid pigments has been isolated from manakins. Brush (1969) extracted the keto-carotenoids, canthaxanthin and astaxanthin, from crown feathers of *Pipra aureola,* which is closely related to *P. filicauda,* a parent of the hybrid described here. In a later analysis employing high-performance liquid chromatography, Hudon et al. (1989) isolated at least nine carotenoid pigments, including xanthophylls and lutein, from the red crown feathers of *P. rubrocapilla.* These data suggest that the crown feathers of *P. filicauda* may be colored by a similar diversity of pigments. In contrast, the tips of the crown feathers are unpigmented in the other parental species, *Pipra pipra.* The yellowish-orange crown of the hybrid manakin probably represents a dilution of pigments present in *P. filicauda.* In an analogous case, Brush (1970) isolated a single carotenoid pigment from the rump feathers of the tanagers, *Ramphocelus flammigerus* (bright scarlet) and *R. icteronotus* (lemon yellow) and their hybrids. He hypothesized that the "orange" rump color in hybrids was due simply to quantitative differences in the amount of the pigment present. In manakins, the expression of "red" may also be dosage dependent. If so, the intermediate crown color of the hybrid may reflect genetic heterozygosity. An alternate hypothesis is that the red pigments of *P. filicauda* are absent in the hybrid leaving only yellow and yellowish-orange pigments in its crown feathers.

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Appendix

Comparative descriptions of the hybrid, *Dixiphia pipra* × *Pipra filicauda*, and its parental species (males in definitive plumage) (see Fig. 1).

The forecrown of *filicauda* is yellow; feathers of the crown, hindneck, and upper mantle are pale yellow broadly tipped with lustrous orangish-red. In *pipra*, the forecrown, crown and upper hindneck are white; the basal fifth of the crown feathers is light gray to medium gray. In the hybrid, the forecrown, crown, hindneck, and scattered feathers of the upper mantle are golden yellow; feathers of the crown have yellowish-orange tips and gray bases.

The mantle, lower back, rump, wings, and tail of *filicauda, pipra,* and the hybrid are glossy black; yellow feathers occur along the bend of the wing in *filicauda* (traces of yellow in the hybrid). Inner webs of the inner remiges of *filicauda* possess large white spots concealed in the folded wing; remiges of *pipra* are uniformly black; those of the hybrid are black with a narrow pale border near the base of the inner web of the secondaries.

The tail of *filicauda* is uniquely modified among the Piprinae; the barbless rachi of the three outer pairs of rectrices extend 30 to 60 mm beyond the tips of the tapered vanes. In *pipra* the tail is slightly rounded; feather tips are broad. The tail of the hybrid is shallowly forked (11 mm) and intermediate in shape. The central rectrices are broadly rounded, the outer rectrices are tapered; rachi do not extend beyond the vanes.

The lores, eye ring, and auriculars are yellow in *filicauda*. In *pipra* the lores and auriculars are black; the white of the crown extends ventrally to the eye ring. The lores, subocular area, and auriculars of the hybrid are grizzled yellow and black producing a distinctive face patch.

In *filicauda* the underparts from the throat to the vent are yellow; the undertail coverts are black; tibial feathers are grayish-black with some yellowish barbules; underwing coverts are yellowish white. The underparts including underwing coverts are black in *pipra*. The underparts of the hybrid are yellow mottled with black. Scattered deposits of melanin can be seen under magnification (30×) in feathers that appear to be entirely yellow; other feathers are visibly mottled, and some near the sides of the breast are predominately black.

The bills of *filicauda, pipra,* and the hybrid are black, whitish along the tomia (in dried skins). Feet and legs of *filicauda, pipra,* and the hybrid are dark blackish-brown (in dried skins).